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# Acanthodians from the Silurian–Devonian boundary beds of Novaya Zemlya Archipelago, Russia

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## ABSTRACT

An acanthodian assemblage is reported for the first time from the Silurian–Devonian boundary beds of Novaya Zemlya Archipelago, Russia. The acanthodian scales and rare other vertebrate microremains were in a sample collected from the Reliktovoe Formation of the western coast of Inostantzev Bay, North Island. The assemblage includes *Gomphonchus mediocostatus*, *Gomphonchoporus hoppei* taxa previously described from the Pridoli – Lochkovian of Laurussia, and *Taimyrolepis composita* occurred in the Lochkovian of Siberia. *Gomphonchus mediocostatus* and *Gomphonchoporus hoppei* are widely distributed in the Baltica palaeogeographic province, and *Taimyrolepis* is known from the Siberia province, indicating connection between those provinces.

## ARTICLE HISTORY

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## KEYWORDS

Acanthodii; Pridoli – Lochkovian; Novaya Zemlya; Russia; *Gomphonchus mediocostatus*; *Gomphonchoporus hoppei*; *Taimyrolepis composita*

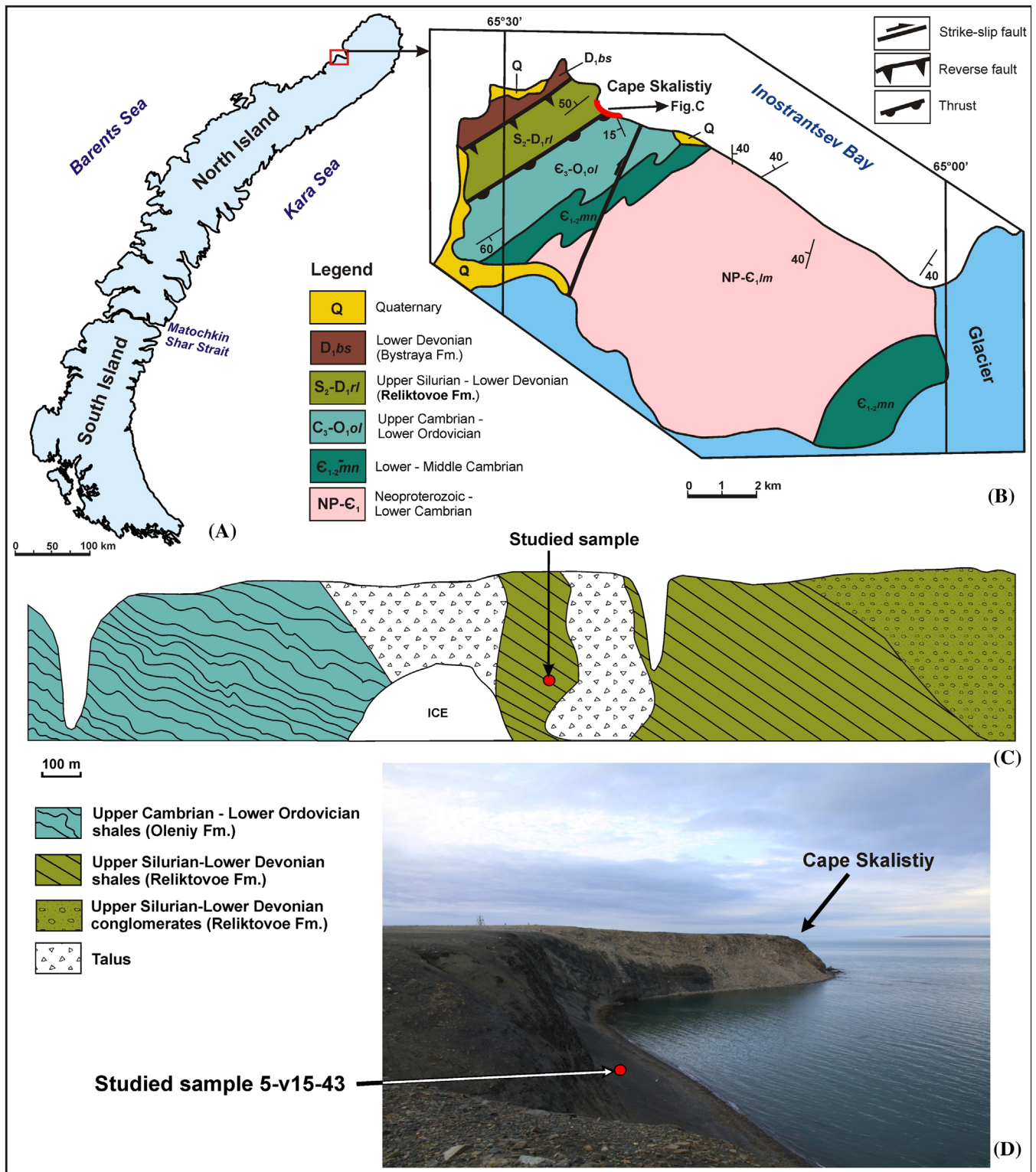
## Introduction

Data on the vertebrates from the Silurian – Lower Devonian of Novaya Zemlya Archipelago are extremely rare. The oldest known collection of Early Devonian fossil fish from Novaya Zemlya was made in 1921 by O. Holtedahl (Nakrem 2007). Obruchev (1973) mentioned the occurrence of sarcopterygian *Porolepis* sp. in the Lower Devonian of Morzhovaya Bay, south-western Novaya Zemlya. Mark-Kurik & Novitskaya (1977) reported vertebrates from the Lochkovian Veselaya Gora Formation of Schmidt Peninsula on North Island, Novaya Zemlya. The assemblage includes two heterostracans resembling *Doryaspis* and *Gigantaspis*, osteostracan *Cephalaspis* sp., placoderm Arctolepidida n. gen., acanthodians and sarcopterygian *Porolepis*? sp. (Mark-Kurik & Novitskaya 1977; Pernègre & Blicek 2016). Two types of acanthodian dermal elements – fin spines and dentigerous jaw bones – were illustrated as outline drawings by Mark-Kurik & Novitskaya (1977, figs. 7–9); they considered the specimens to possibly be from new genera, but noted the similarity of the noded-ridged spines with those of climatiid acanthodians from the Welsh Borderland. We recognise this form (Mark-Kurik & Novitskaya 1977, fig. 7) as most similar to spines of *Nostolepis* spp. from the late Silurian–Lochkovian of the Baltic (Gross 1971, pl. 8) and the Welsh Borderland (Newman et al. 2017, fig. 8F). The fin spines with four flat smooth ridges on each side (Mark-Kurik & Novitskaya 1977, fig. 8) resemble those assigned by Gross (1971, pl. 9.1, 2) to the ischnacanthid *Gomphonchus*?, and also those of *Ischnacanthus* spp. from the Lochkovian of Scotland (Watson 1937, fig. 10) and the Welsh Borderland (White 1961, pl. 45.4). The jaw bone

fragment (Mark-Kurik & Novitskaya 1977, fig. 9) is comparable with those of acritolepid and poracanthodid ischnacanthiforms (e.g., Valiukevičius 1992, 2003a) from the Lochkovian of Severnaya Zemlya. Thelodonts have also been described from Novaya Zemlya, including *Thelodus sculptilis* and *T. sp.* from the late Silurian; *Turinia pagei*, *T. polita* and *Nikolivia* sp. from the Lochkovian Kamenka Bay Regional Stage, and *Amaltheolepis winsnesi* from the Emsian Sinelnikov Regional Stage (Karatajute-Talimaa 2000; Cherksova et al. 2000). The heterostracan *Tolypelepis* sp. was found in the upper Silurian Konstantin Formation of North Island (Shkarubo 2013).

Early Devonian acanthodians have been described from several Arctic regions that were relatively close by at the time, including: Severnaya Zemlya: acanthodian articulated fish and isolated scales described by Valiukevičius (1992, 1994, 2003a); Spitsbergen: acanthodian scales, jaw bones and fin spines reported by Ørvig (1957, 1969), Blicek et al. (1987), Ilyes (1995) and Harland (1997), plus Pragian–Emsian acanthodian trace fossils *Undichna* by Wisshak et al. (2004); and Chukotka: rare acanthodian scales described by Mark-Kurik et al. (2013). The late Silurian–Early Devonian acanthodians from the Baltic countries, on the other hand, have been extensively described, starting with Pander (1856).

A new vertebrate assemblage including the acanthodian scales described below was found during the expedition of Karpinskiy Russian Geological Research Institute (St. Petersburg, VSEGEI), supported by Ministry of Mineral Resources of Russia, in 2015 in the region of Inostantzev Bay, North Island of Novaya Zemlya Archipelago.



**Figure 1. A, B.** Maps showing the location of the studied section on North Island, Novaya Zemlya. **C.** Geological section of coast outcrop at Cape Skalistiy. **D.** Photograph of studied outcrop with position of fish sample.

### Geological setting

Novaya Zemlya Archipelago is the largest archipelago of the Russian Arctic, located in the Arctic Ocean surrounded by the Barents and Kara seas. It consists of two large islands, South and North, separated by Matochkin Shar strait. Novaya Zemlya is structurally part of the Uralian Orogen Belt. The archipelago

represents the exposed crustal fragment formed as a result of Early Mesozoic orogeny. Novaya Zemlya was the northern part of Baltica in the Silurian and Early Devonian.

The studied area is situated in the northernmost part of the archipelago, on the western coast of Inostantzev Bay, Barents Sea (Fig. 1A, B). This area comprises the variously deformed strata of the

latest Neoproterozoic (?) to Devonian. The latest Neoproterozoic (?) – Middle Cambrian deposits are intensively deformed alternating argillites, siltstones with subordinate beds of sandstones and limestones (in the upper part of the succession). The intensively deformed Upper Cambrian – Lower Ordovician strata comprise black shales with rare beds of limestones. The upper Silurian – Lower Devonian Reliktovoe Formation is represented by weakly deformed black shales, argillites and siltstones with rare beds of clayey limestones and thick beds of conglomerates at the top of the succession. The Reliktovoe Formation was dated by a brachiopod assemblage as Pridoli – Lochkovian (Bondarev & Andreeva 1981; Guo et al. 2010). The overlying Lower Devonian Bystraya Formation includes limestones with interlayers of dolomites, siltstones and sandstones. The formation contains corals, brachiopods and ostracods which indicate the age as the Lochkovian – Pragian (Bondarev & Andreeva 1981; Guo et al. 2010).

The sample 5-v15-43 which yielded the studied fish microremains was collected from the thin layer of clayey limestone within black shales of the upper Silurian-Lower Devonian Reliktovoe Formation in outcrop near Cape Skalistiy (Fig. 1 C, D).

## Material and methods

The studied scales of acanthodians were obtained from acid-treated samples collected for microfauna. The fish microremains were micrographed on the scanning electron microscopes Cambridge CamScan-4 and Tescan VEGA-II XMU. Thin sections of selected scales were imaged using an Olympus BX-50 transmission microscope and DP-12 imaging system. The specimens are housed in the Paleontological Museum of St. Petersburg State University, St. Petersburg, Russia (PM SPU 92).

## Systematic palaeontology

### CLASS ACANTHODII OWEN, 1846

#### ORDER ISCHNACANTHIFORMES BERG, 1940

#### FAMILY ISCHNACANTHIDAE WOODWARD, 1891

#### Genus *Gomphonchus* (PANDER, 1856)

*Type species*: – *Gomphodus sandelensis* (Pander, 1856)

*Gomphonchus mediocostatus* Vergoossen, 1999a (Fig. 2)

*Material*. – At least 28 scales including PM SPU 92-1 – 92-12 and two scale thin sections; western coast of Inostantzev Bay, North Island, Novaya Zemlya; sample 5-v15-43, Reliktovoe Formation, upper Silurian-Lower Devonian.

*Description*. – The scales are from 0.3 mm (Fig. 2A, B) to 0.9 mm (Fig. 2C) long and wide, with most being slightly wider than long, and up to 0.7 mm high. The crown surface is flat and horizontal, and in nearly all scales the anterior margin is curved and sharply demarcated. The crown is ornamented with two (Fig. 2A) to seven (Fig. 2C, D) subparallel ridges running from the anterior edge into the posterior half of the crown, often to the posterolateral edges. On some scales the ridges tend to converge towards the posterior corner (Fig. 2B), rather than being subparallel. The ridges are sharp-crested, in rare instances they bifurcate anteriorly (Fig. 2E, F). The two median ridges are more widely separated than the other ridges on some scales (Fig. 2F, G), but mostly the ridges are more or less equally spaced. Some scales have one or two oblique ridges lateral to the main subparallel

ridges, running from the anterior edge towards the more medial ridges (Fig. 2E, H). Most scales have straight posterolateral edges converging at about 80°, but some scales have “staggered” posterolateral edges (Fig. 2C, F). The crown growth layers are sometimes visible in the posterior half of the crown, particularly on scales with shorter ridges, possibly caused by abrasion; about four growth zones are discernible (Fig. 2I). The scale neck is deep and concave all round, with vertical ridges (“buttresses”) posteriorly between canal openings (Fig. 2J). A sharp rim separates the neck from the base, which is moderately convex with its greatest depth forward of centre (Fig. 2E). The base is slightly wider than the crown. One scale has a straight anterior crown margin that parallels the anterior edge of the base (Fig. 2K).

A detached scale crown (Fig. 2L) and another whole scale were sacrificed for thin sectioning (Fig. 2M, N). Histological structure of the scale crowns corresponds to the *Gomphonchus* type, as described by Gross (1971), with dense orthodentine-like tubules filling the crown growth zones (Fig. 2M). Scale bases have mostly been recrystallised (Fig. 2N), obscuring the original structure.

*Comparison*. – Valiukevičius (2003b) described the histological structure of *G. mediocostatus* scales as having bushy and uniform ascending vascular canals in the crown, frequently without main branches, numerous thin growth lamellae and completely acellular bone in the bases. The features preserved in the Novaya Zemlya scales (i.e., the dentine) appear comparable to those listed by Valiukevičius (2003b) as distinguishing this species from the closely related *G. minicostatus* Valiukevičius, 2003.

*Occurrence*. – Erratic limestones (upper Pridoli) from the northern Netherlands (Vergoossen 1999a); ? Man Brook 7 locality (uppermost Pridoli), Welsh Borderland, UK (Vergoossen 1999a, 1999b, 2000); Jūra, Rietavas and Lapės formations (upper Pridoli) and Tilžė Formation (Lochkovian), Lithuania (Valiukevičius 2003b, 2005); Greben’ Regional Stage (Pridoli), Timan – Pechora Province, Russia (Valiukevičius 2003b); Reliktovoe Formation (Pridoli–Lochkovian), Inostantzev Bay, Novaya Zemlya.

#### FAMILY PORACANTHODIDAE VERGOOSSEN, 1997

#### Genus *Gomphonchoporus* VERGOOSSEN, 1999a

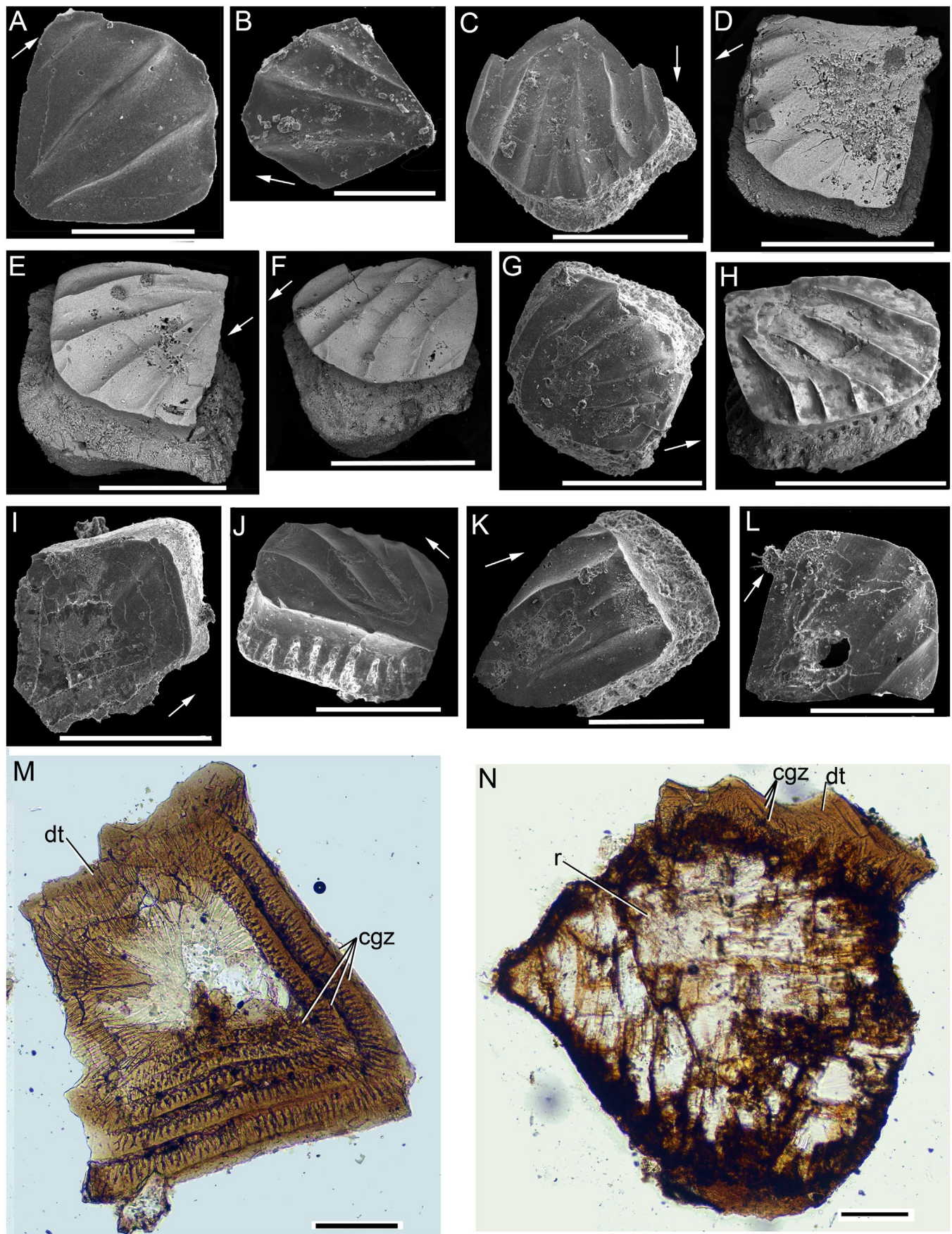
*Gomphonchoporus hoppei* (Gross, 1971) (Fig. 3A–C)

*Material*. – Four scales including PM SPU 92-13 – 92-15; western coast of Inostantzev Bay, North Island, Novaya Zemlya; sample 5-v15-43, Reliktovoe Formation, upper Silurian-Lower Devonian.

*Description*. – The scales are 0.7–1.0 mm wide. Scale crowns are poorly preserved (especially Fig. 3A), but appear relatively flat, with up to ten short radial ridges (Fig. 3B) along the rounded anterior margin. When preserved, the posterior crown extends behind the posterior corner of the base (Fig. 3C). Scale bases are broader than long, and broader than the crown; the base is as deep as the crown plus neck, and is somewhat lemon-shaped in dorsal or ventral view.

*Comparison*. – Valiukevičius (1998) listed occurrences of *Gomphonchus hoppei* and *Gomphonchus* aff. *hoppei* in the Pridoli–Lochkovian of the Baltic; he distinguished the latter from the former by the “lack of lowered distal area on the crown with pore canal openings” (Valiukevičius 1998, p. 41). The few specimens we have from Novaya Zemlya correspond to

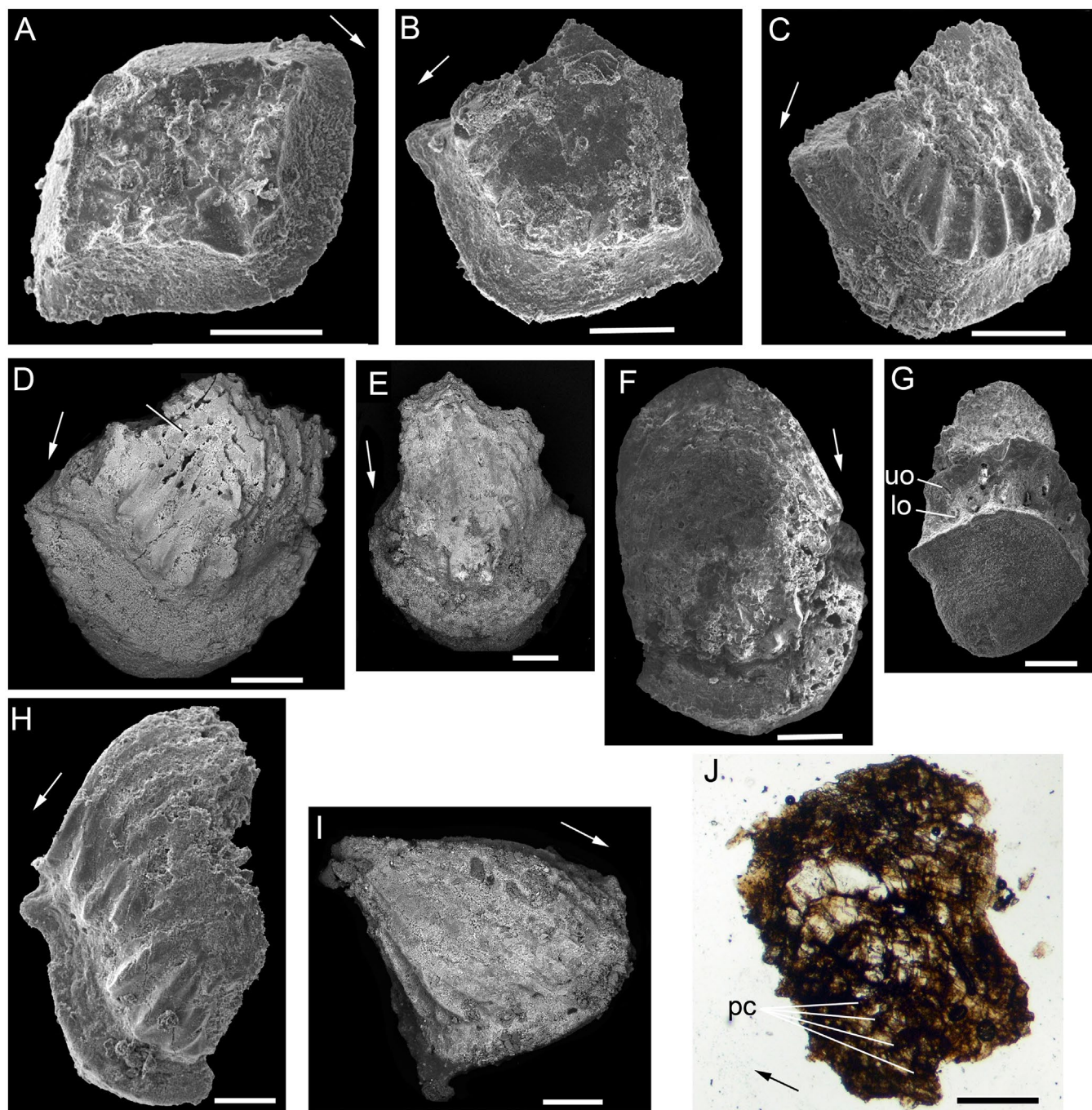




**Figure 2.** *Gomphonchus mediocostatus* Vergoossen, 1999 scales, Reliktovoe Formation of Novaya Zemlya. **A.** PM SPU 92-1, crown view; **B.** PM SPU 92-2, detached crown, crown view; **C.** PM SPU 92-3, crown view; **D.** PM SPU 92-4, crown view; **E.** PM SPU 92-5, laterocrown view; **F.** PM SPU 92-6, anterocrown view; **G.** PM SPU 92-7, crown view; **H.** PM SPU 92-8, laterocrown view; **I.** PM SPU 92-9, crown view; **J.** PM SPU 92-10, posterocrown view; **K.** PM SPU 92-11, crown view; **L.** PM SPU 92-12, crown view; **M.** NZ\_1, horizontal section of crown; **N.** NZ\_2, oblique vertical section.

Notes: A–L are SEM images. Abbreviations: cgz, crown growth zones; dt, dentine tubules; r, remineralisation. Scale bars = 0.1 mm in M, N; 0.2 mm in A, B; 0.3 mm in E, K, L; 0.5 mm in C, D, F, G, H, J, J.





**Figure 3.** Poracanthodid acanthodian scales from the Reliktovoe Formation of Novaya Zemlya. A–C, *Gomphonchoporus hoppei* (Gross, 1971). A. PM SPU 92-13, crown view; B. PM SPU 92-14, crown view; C. PM SPU 92-15, crown view. D–J, *Taimyrolepis composita* Valiukevičius, 1994. D. PM SPU 92-16, crown view; E. PM SPU 92-17, crown view; F. PM SPU 92-18, crown view; G. PM SPU 92-19, posterobasal view; H. PM SPU 92-20, crown view; I. PM SPU 92-21, laterocrown view; J. NZ\_3, horizontal section of crown.

Notes: A–I are SEM images; arrows indicate anterior direction. Abbreviations: lo, lower neck canal opening; pc, row of crosscut pore canals; uo, upper neck canal opening. Scale bars = 0.2 mm.

the latter group. Vergoossen (1999a) regarded both scale forms as variants of *Gomphonchoporus hoppei*, based on the occurrence of well-preserved specimens of all morphovariants in an erratic boulder, and the gradation between the forms. Following Vergoossen (1999a), the Novaya Zemlya scales correspond to Gross' (1971) morphological form type (1). Vergoossen (1999a) erected the new genus *Gomphonchoporus*; the presence of a pore canal system in some of the scale variants indicated the taxon should be assigned to the Poracanthodidae rather than

the Ischnacanthidae, as the latter do not have pore canals. This necessitated the erection of a new genus, because *Gomphonchus* spp. lack a pore canal system. Subsequently Valiukevičius (2005) tabled occurrences of *Gomphonchus hoppei* and *Gomphonchus* sp. cf. *G. hoppei* in the Jūra Formation, Lithuania, but did not specify how he distinguished between the two. It seems possible that the latter taxon is the descriptor for the same scales which he variously labelled *Gomphonchus* aff. *hoppei* or *Gomphonchus* cf. *hoppei* in earlier papers (e.g., Valiukevičius 1998, 2000, 2004).

We follow Vergoossen (1999a), and assign all these variants to the same taxon, *Gomphonchoporus hoppei*.

**Occurrence.** – Erratic limestones (upper Pridoli) from the northern plains of Germany and the Netherlands (Gross 1971; Vergoossen 1999a); Pridoli, Poland and Central Urals (Märss 1997); Man Brook 7 locality (uppermost Pridoli), Welsh Borderland, UK (Vergoossen 1999a, 2000); Jūra, Rietavas and Lapės formations (upper Pridoli) and Tilžė Formation (Lochkovian), Lithuania (Valiukevičius 2003b, 2005); and Borschevo Regional Stage (Lochkovian), Belarus (Plax 2011, 2015); Greben' Regional Stage (Pridoli), Timan – Pechora Province, Russia (Valiukevičius 2003b); Reliktovoe Formation (Pridoli–Lochkovian), Inostantzev Bay, Novaya Zemlya.

Genus *Taimyrolepis* Valiukevičius, 1994

**Diagnosis** (based on Valiukevičius translation in 1995, pers. comm.). – Large scales (0.7–1.25 mm) with compound ridged crown. Five to seven rough, smooth, parallel or fan-like ridges prolonged through the whole crown. Three to four medial ridges may grow together and make a higher area. At the distal edge they are lower, cut by cross grooves with openings of pore canals. Histological structure of “Nostolepis” type. Oriented mesodentine is lacking. The simple mesodentine of the crown (3–4 growth lamellae) is pierced by narrow dentine canals with lacunae. Wide main branches of canals are not seen. The thin-layered bone of the base contains rare osteocyte cavities.

*Taimyrolepis composita* Valiukevičius, 1994

(Fig. 3D–J)

**Material.** – Eight scales including PM SPU 92-16 – 92-21 and one scale thin section; western coast of Inostantzev Bay, North Island, Novaya Zemlya; sample 5-v15-43, Reliktovoe Formation, upper Silurian–Lower Devonian.

**Description.** – The scales are 0.8 to 1.2 mm wide. The anterior margin of the crown is strongly curved in outline, and rises up directly from the neck/base (Fig. 3D–F). Up to ten ridges radiate back from the anterior edge. Serrated-edged plates overlap to form the crown posterior to the ridges (Fig. 3D,E). Pore openings are rarely visible between the plates; possibly these are only exposed through erosion of the crown, which is poorly preserved. The neck is relatively deep posteriorly, and penetrated by canal openings under the posterior crown overhang and across the middle of the neck (Fig. 3G). The sharp neck-base rim is oval to lemon shaped in outline, and the base is deep. A few scales differ from this general form: one is wide with a sinuous anterior margin (Fig. 3H), and another is more dorso-ventrally flattened (Fig. 3I) than the normal presumed flank scales.

**Histology.** Unfortunately, the whole of the scale sacrificed for sectioning (Fig. 3J) was remineralised, obscuring the internal structure. Parallel unbranching dentine tubules extend through the crown growth zones posteriorly, and radial lines of pore canals are also present in the posterior crown. The poor preservation of the crowns as well as the bases indicates that the upper levels of the crown tissue is less highly mineralised than in scales of *G. mediocostatus*.

**Comparison.** – Valiukevičius (1988) originally assigned this scale form to *Machaeracanthus*?, but scales of *Machaeracanthus* lack a pore canal system (Gross 1973; Burrow et al. 2013). Burrow et al. (2013) erected a new genus *Machaeraporus* for scales

from the Pridoli of Nova Scotia, Canada originally assigned to *Cheiracanthoides stonehousensis* Legault, 1968, which have a pore canal system, but in *Machaeraporus* the canals only open out on the underside of the posterior crown, not the surface. Crown morphology of the Novaya Zemlya scales is similar to that of *Radioporacanthodes liujingensis* (Wang, 1992) from the Pragian – early Emsian of Guangxi county, China, but the latter differ in having sharp-crested crown ridges and a very high neck anteriorly (Wang 1992, pl. 3 fig. 1b; Burrow et al. 2000, pl. 2 fig. 7), pore canal openings only in the posterior third of the crown, and in lacking overlapping layers forming the posterior crown (as far as can be estimated by the few known well-preserved scales of *R. liujingensis*). Because the crown ornament and histological structure are poorly preserved in the Novaya Zemlya scales, a close comparison with scales from other taxa is limited to their general shape and morphology, and these fall within the range shown by the type material of *T. composita*. Valiukevičius (1994) compared the structure of the posterior crown with that in *Gomphonchus hoppei* (as noted above, this species is now referred to *Gomphonchoporus hoppei*), but noted that the latter species only has radial ridges, without diverging ridges on the lateral areas of the crown (Fig. 3D, I). Well-preserved scales in a late Pridoli East Baltic – derived erratic limestone from the northern Netherlands, one of which Vergoossen (1999a, figs. 42–44) nominated as neotype for *Gomphonchoporus hoppei*, show a similar structure in the posterior crown to that in some of the Novaya Zemlya scales, with overlapping growth zones. The *G. hoppei* scales differ in having straight posterolateral edges on most of the growth zones, with serrated/zigzag edges only on the youngest zone, if present at all. On *T. composita* scales, all the posterior growth zones have serrated/zigzag edges. The two species also differ in the extent of the scale pore canal system, which is only present in one of the *G. hoppei* morphotypes, where it is limited to the posterolateral areas of the crown. In *T. composita* type material, the pore canal system comprises large branching sinuous canals that penetrate the scale base as well as the crown (Valiukevičius 1994, fig. 72.4); we cannot determine the presence or absence of this feature in the Novaya Zemlya scales, but consider their morphology is distinctive enough to assign to this species.

**Remarks.** – Valiukevičius (1988) originally considered this species to possibly belong to *Machaeracanthus*, before erecting a new genus and species *Taimyrolepis composita* Valiukevičius, 1994, assigned to the Order Climaatiiformes, Family Climaatiidae. This order is no longer considered valid (e.g., Burrow 2002), and *Taimyrolepis* does not show any diagnostic characters to support assigning it to the Climaatiidae. Indeed, the pore canal system identified within the crown and base of *T. composita* scales indicate the species should rather be assigned to the poracanthodid ischnacanthiforms.

**Occurrence.** – Uryum Beds, Ust' Tareya Regional Stage (Lochkovian), Tareya River, Taimyr Penninsula, Russia (Valiukevičius 1994); Reliktovoe Formation (Pridoli–Lochkovian), Inostantzev Bay, Novaya Zemlya.

## Discussion

Although the acanthodian scale assemblage from Reliktovoe Formation of western coast of Inostantzev Bay, North Island, Novaya Zemlya is limited in abundance and diversity, the taxa present indicate a latest Pridoli – earliest Lochkovian age based



on their stratigraphic distribution elsewhere. *Gomphonchoporus hoppei* s.s. is recorded throughout the Baltic countries (Valiukevičius 2000), Belarus (Plax 2015), Poland, Central Urals, Russia (Märss 1997) and probably Severnaya Zemlya Archipelago (Valiukevičius 2003a); plus the Welsh Borderland, UK (Vergoossen 1999a), first appearing in the lower Pridoli (Jura Regional Stage) in Lithuania (Valiukevičius 2005, fig. 7) and ranging up to the middle Lochkovian (Valiukevičius 2000, fig. 1). *Gomphonchus mediocostatus* is recorded from the Baltic countries and the Welsh Borderland, but is only recorded from the uppermost Pridoli to Lochkovian (Vergoossen 1999a; Valiukevičius 2005, fig. 7). *Taimyrolepis composita* is known from the Lochkovian of Tareya River, Taimyr Penninsula. The acanthodian macroremains described by Mark-Kurik & Novitskaya (1977) are not very helpful in assessing the palaeogeography at a slightly younger time (upper Lochkovian), because we only recognise the taxa in their descriptions at a suprageneric level, or from a widespread genus (*Nostolepis*).

The acanthodian fauna from the Pridoli – Lochkovian of Novaya Zemlya includes two taxa *Gomphonchus mediocostatus* and *Gomphonchoporus hoppei* widely distributed in the southern Baltica palaeogeographic province and one species *Taimyrolepis composita* which occurred in the Siberian province. During the late Silurian – early Devonian, Novaya Zemlya and the Ural Mountains formed the northern margin of Baltica (Cocks & Torsvik 2005), with a relatively wide ocean separating the land areas of Baltica and the Siberian terrane (Cocks & Torsvik 2016, fig. 8.1a). The invertebrate faunas from the Pridoli – Lochkovian of Novaya Zemlya are close in taxonomic composition to those from the Urals and the Timan-Pechora Province as well as from Severnaya Zemlya (e.g., Modzalevskaya 1985; Nekhorosheva & Patrunov 1999; Abushik & Evdokimova 1999), and heterostracan agnathan faunas from Spitsbergen, Novaya Zemlya and Severnaya Zemlya show close similarities during the Early Devonian (Pernègre & Blicek 2016). Unfortunately, although acanthodians have been recorded as commonly occurring in the Lochkovian Red Bay Group in west Spitsbergen (Ørvig 1969; Blicek et al. 1987), the material has not been systematically described or figured, being mostly nominally assigned to the genera “*Nostolepis*”, “*Gomphonchus*”, and “*Onchus*”. A poorly preserved and sparse acanthodian fauna is known from Chukotka (Mark-Kurik et al. 2013), but none of the species recorded there are represented in the Novaya Zemlya fauna.

Whereas the distribution of most faunas was restricted to the continental shelf areas of the different terranes, acanthodians were nektonic and able to migrate across deeper waters. The distribution of *Taimyrolepis composita* indicates the northern Baltica and Siberia terrane faunas at that time could have been connected via Severnaya Zemlya and Taimyr.

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## Disclosure statement

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